

# A COMPARATIVE STUDY ON THE CILIARY FEEDING MECHANISMS OF ANADARA SPECIES FROM DIFFERENT HABITATS

C. F. LIM

*Dept. of Zoology, University of Singapore, Singapore*

Ciliary currents and feeding mechanisms in the mantle cavity of bivalves have been extensively studied (Kellogg, 1915; Atkins, 1936; others). One of the first to observe such ciliation in members of the Arcacea was Stenta (1903), who noted the peculiar occurrence of a posteriorly-directed rejection current along the ventral edge of the ctenidia in *Arca*. Atkins (1936) examined in detail the currents associated with the ctenidia, palps, visceral mass, and mantle of *Glycymeris glycymeris* (L.) and *Arca tetragona* Poli and reported the presence of latero-frontal cilia in both these species. About 20 years later Yonge (1955) found that the inhalant and exhalant currents were restricted to the posterior region in "*Arca senilis* Lam." (= *Anadara senilis* L.). Purchon (1956) has briefly described the ctenidia, palp, and mantle ciliation in *Anadara granosa* (L.), and reported an anteriorly-directed ciliary current along the ventral ctenidial edge instead of a posteriorly-directed rejection current which is apparently universal within the Arcacea. Recently the general pattern of the ciliary currents has been examined in *Anadara trapezia* (Deshayes) by Sullivan (1961), who confirmed the findings of Atkins (1936).

In this study the ciliary feeding mechanisms of three species of *Anadara* from three different habitats (namely, rocky, sandy, and muddy) were investigated to find out if there were any significant differences. Observations were also made on *A. granosa* previously studied by Purchon (1956).

## MATERIALS AND METHODS

Specimens of *Anadara antiquata* (L.), *A. anomala* (Reeve), and *A. cuneata* (Reeve) were collected from rocks, sand, and mangrove mud in Singapore at Tanjong Gul, Bedok, and Seletar, respectively. They were all obtained from the intertidal zone of the shore and examined in the Department of Zoology, University of Singapore. Specimens of *A. granosa* were obtained from Singapore markets.

Living specimens in sea water were treated with particles of animal charcoal, carborundum and carmine, and the movements of these particles were studied under the microscope. In all cases the right valve, including the right mantle lobe, was first carefully removed before observations were made within the mantle cavity. After these *in situ* studies, portions of the ctenidia and labial palps were excised and examined separately under the microscope in the same manner.

The inhalant and exhalant currents through the mantle cavity of intact living animals were investigated in small glass tanks. Carmine particles were employed

and the conditions in the tanks were made to resemble those in the field as far as possible.

## RESULTS

### FIELD OBSERVATIONS

The three species, *Anadara antiquata*, *A. anomala*, and *A. cuneata*, were observed to exhibit vertical zonation, although occasional individuals may be found in any part of the shore that is inundated. *A. cuneata* occurs between mean sea-level and high water of spring tides. *A. antiquata* usually occurs around mean sea-level. *A. anomala* is restricted to areas below mean sea-level.

*Anadara antiquata*, being a rocky-shore inhabitant, is usually found attached to rocks and stones by means of its slender byssus. Its position is variable, depending upon the contour of the rock or stone to which it is anchored. In any case the posterior portions of the animal are nearly always more or less oriented towards light (Fig. 1A). The byssus is detached very easily if not carefully handled. The

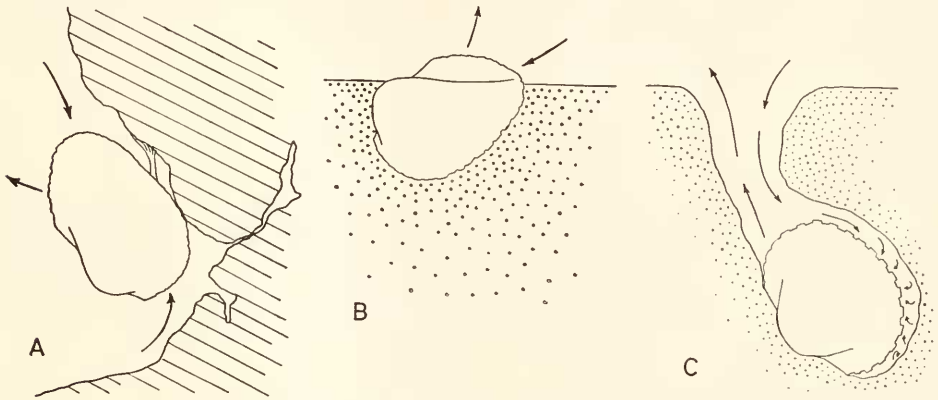


FIGURE 1. Water currents entering and leaving the mantle cavity (position in life). A. *Anadara antiquata* (L.). B. *Anadara anomala* (Rve.). C. *Anadara cuneata* (Rve.).

### ABBREVIATIONS USED FOR FIGURES 1 TO 5

A, anus; AI, amoebocyte; AA, anterior adductor muscle; AID, ascending limb of inner demibranch; AOD, ascending limb of outer demibranch; ARM, anterior retractor muscle; B, byssus; BG, byssal groove; BS, blood sinus; CFC, coarse frontal cilia; CJ, ciliary junction; CT, connective tissue; DID, descending limb of inner demibranch; DOD, descending limb of outer demibranch; E, "eye" spots on edge of mantle lobe; F, foot; FFC, fine frontal cilia; GA, gill axis; IE, inner epithelium; IF, inner fold of labial palp; IS, infra-filamental septum; LID, left inner demibranch; LC, lateral cilia; LM, left mantle lobe; LOG, lateral oral groove; M, mouth; MF, membranous fold of labial palp; MF1, muscle fiber; MG, mucous gland cell; MG1, mucous gland cell of first type; MG2, mucous gland cell of second type; MG3, mucous gland cell of third type; NE, nucleated erythrocyte; OE, outer epithelium; OFC, orally directed food current; OP, outer fold of labial palp; PA, posterior adductor muscle; POG, proximal oral groove; PRC, posteriorly directed rejection current; PRM, posterior retractor muscle; RIP, inner fold of right labial palp; ROD, right outer demibranch; ROP, outer fold of right labial palp; RP, portion of right labial palp; SM, suspensory membrane; TF, transverse fold of labial palp; TG, transverse groove of labial palp; VM, visceral mass; X, point of rejection of particles; Y, point of entry of current from outer surface of palp.

point of detachment is close to its origin within the byssal groove. When the animal is dislodged, it moves with the help of its muscular foot and re-attaches itself with the secretion of a new byssus. Frequently, a commensal crab (*Pinnotheres* sp.) is seen living in the mantle cavity of the bivalve.

Unlike *A. antiquata* the species *A. anomala* lies buried with the greater part of its body embedded in the sand, with only a little of the posterior end protruding above the surface (Fig. 1B). Growths of algae and tiny barnacles often encrust the exposed posterior end of the shell. The byssus is absent. Although the former species (*A. antiquata*) may be wholly exposed to air at low tide, *A. anomala* never experiences complete exposure. It remains in its semi-buried position most of the time and is not observed to change its burrow unless dislodged. *A. anomala* is usually found on sandy shores, where the closely related burrowing species, *A. inaequivallis* (Bruguere), also occurs.

The large species *A. cuneata* lives in the estuarine mangrove mud of Seletar and some parts of the Johore Straits. Unlike the two previous species, it lies completely buried in mud. It is a shallow burrower and is found 6–10 cm. below the mud surface. The entrance to the burrow is irregular in shape and measures roughly 2–3 cm. in diameter. In its shallow burrow, the bivalve lies with its ventro-posterior facing uppermost (Fig. 1C).

#### *Currents entering and leaving the mantle cavity*

##### A. *Anadara antiquata*

The currents leaving and entering the mantle cavity resemble very closely those of *Glycymeris glycymeris* and *Arca tetragona* as observed by Atkins (1936). There are two major inhalant currents and one exhalant current (Fig. 1A). The inhalant currents appear at the anterior and ventro-posterior regions and the exhalant one is observed at the dorso-posterior region of the valves.

##### B. *Anadara anomala*

There are a single inhalant current (as contrasted to two in *A. antiquata*) and one exhalant current. Both the inhalant and exhalant currents lie posteriorly (Fig. 1B) as in *A. senilis*, which was studied by Yonge (1955).

##### C. *Anadara cuneata*

The results of observations on this species agree with those obtained by Sullivan (1961) for *A. trapezia*. There is present a distinct exhalant current at the dorso-posterior region while the inhalant current appears to enter the mantle cavity diffusely throughout the ventral margin of the shell. However, the major part of the inhalant water appears to enter the anterior region of the ventral gape (Fig. 1C).

#### *The ctenidia and their ciliary currents*

##### *Structure*

The anatomy and histology of the ctenidia of *A. antiquata*, *A. anomala* and *A. cuneata* show the general characters of the filibranch gill as observed by Ride-

wood (1903). In all three species studied, latero-frontal and aboral cilia are absent. There are no significant differences in the anatomy and histology of the ctenidia among each of the three species in this study and *A. trapezia* as described by Sullivan (1961).

Some slight anatomical and histological differences do occur among the three species investigated. Comparatively the size of the ctenidia is largest in *A. cuneata*—volume for volume of mantle cavity. There is no appreciable difference in the size of the ctenidia in *A. antiquata* and *A. anomala* (see Figs. 3E, 4E and 5E). The position, shape and flexure of the demibranchs are very similar in each of the three species. The fine frontal cilia are fewer in number in *A. antiquata* than in *A. cuneata*, with *A. anomala* having an intermediate number. Consequently, there

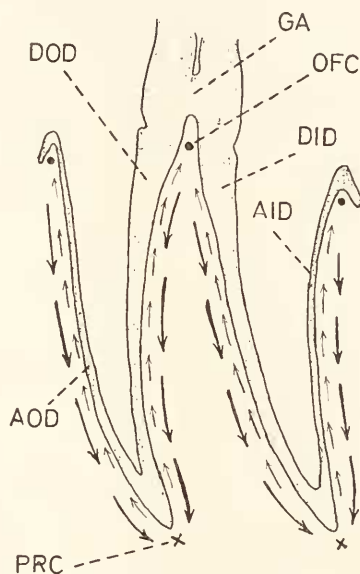


FIGURE 2. Semi-diagrammatic transverse section of ctenidium, showing the direction of the ciliary currents in *Anadara*.

is a proportionate migration of the lateral cilia from a more peripheral region in *A. antiquata* to a more central position in *A. cuneata*. The lateral cilia in *A. anomala* show more or less an intermediate condition between the other two species (Figs. 3A, 4A, and 5A).

#### *The ciliary currents*

Stenta (1903) and later Atkins (1936) found that, unlike the usual anteriorly directed current along the ventral margin of the ctenidia, the marginal current in *Arca* was directed posteriorly. The tract with posteriorly-directed ciliary currents was also noted by Yonge (1955) and Sullivan (1961) for *Anadara senilis* and *A. trapezia*, respectively. The three species of *Anadara* here studied have also been found to show this peculiarity (Figs. 2, 3E, 4E, and 5E). The dorsal, orally

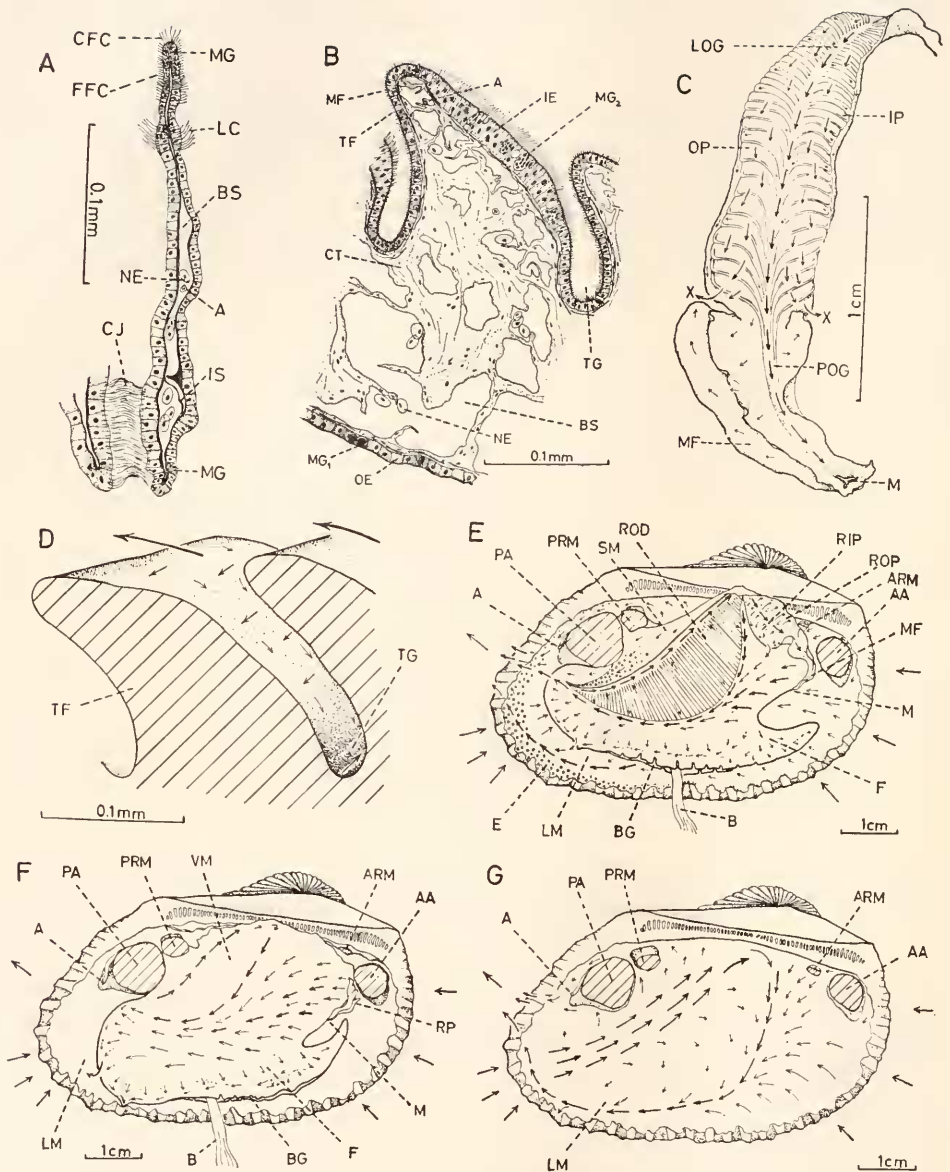


FIGURE 3. *Anadara antiquata* (L.). A. Transverse section of gill filament. B. Transverse section through transverse fold of labial palp. C. Ciliary currents of the left labial palp. D. Currents on two adjacent folds of labial palp (diagrammatic). E. Currents on ctenidium and adjacent areas. F. Currents on the foot and visceral mass. G. Currents on the left mantle lobe.



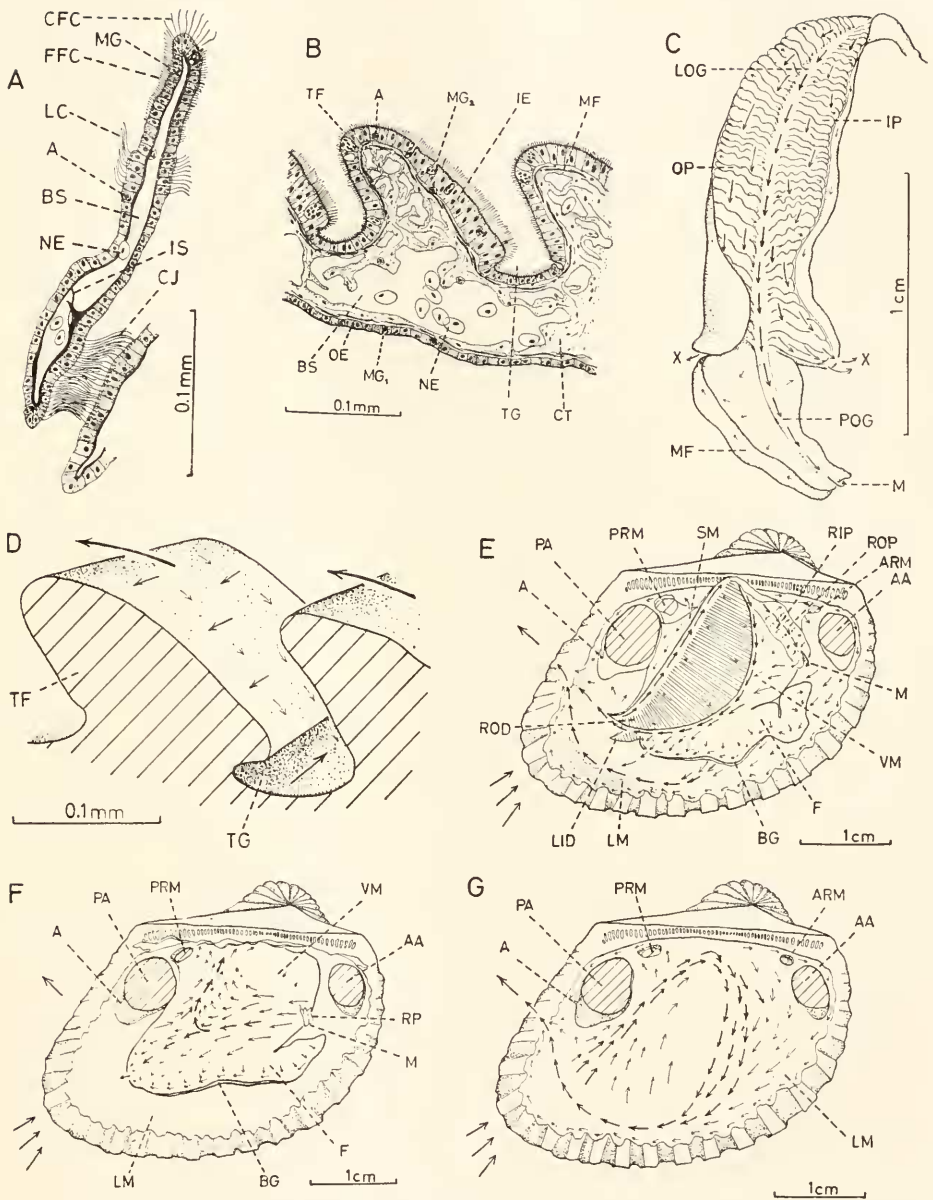


FIGURE 4. *Anadara anomala* (Rve.). A. Transverse section of gill filament. B. Transverse section through transverse fold of labial palp. C. Ciliary currents of the left labial palp. D. Currents on two adjacent folds of labial palp (diagrammatic). E. Currents on ctenidium and adjacent areas. F. Currents on the foot and visceral mass. G. Currents on the left mantle lobe.

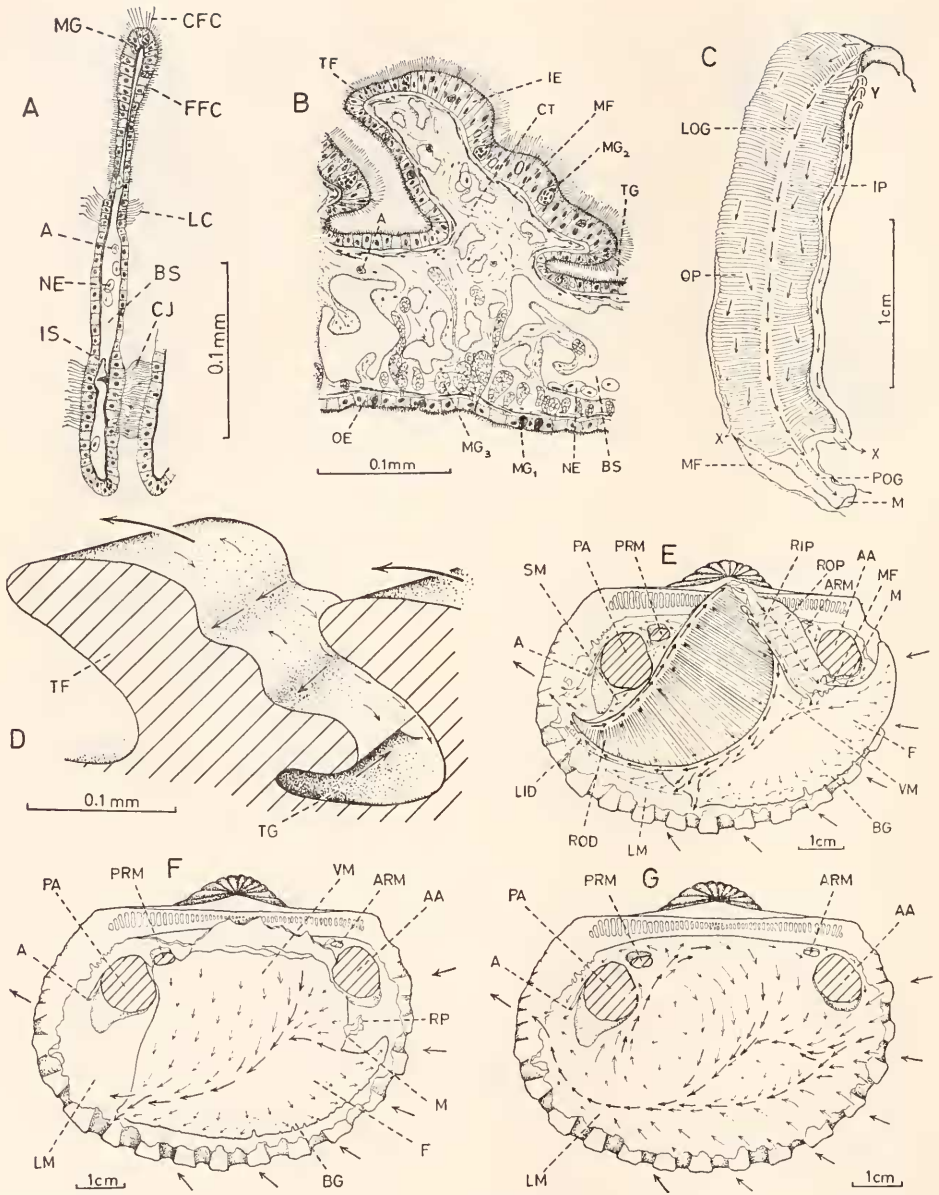


FIGURE 5. *Anadara cuneata* (Rve.). A. Transverse section of gill filament. B. Transverse section through transverse fold of labial palp. C. Ciliary currents of the left labial palp. D. Currents on two adjacent folds of labial palp (diagrammatic). E. Currents on ctenidium and adjacent areas. F. Currents on the foot and visceral mass. G. Currents on the left mantle lobe.

directed, food (ciliary) current and the sorting (ciliary) currents of the gill lamellae of *A. antiquata*, *A. anomala* and *A. cuneata* were all similar to those observed by Atkins (1936) in *Glycymeris* and *Arca*.

My own observations of the ciliary currents in *A. granosa* show that the ciliary current on the ventral margin of the ctenidia in this species is the reverse of what was reported by Purchon (1956); his "weak (food) ciliary current" (Purchon 1956, p. 64) is in fact a strong posteriorly directed rejection current.

### *The labial palps and their sorting mechanisms*

#### A. Structure

The labial palps show more differences among *A. antiquata*, *A. anomala* and *A. cuneata* than the gills. The ventral tips of the anterior filaments of the inner demibranchs of all the three species examined are not inserted into the distal oral groove of the labial palp. This ctenidium-palp association would be classified under Category III of Stasek (1963).

There are significant interspecific differences in the number of the three species examined. *A. antiquata* has 40, *A. anomala* has 43, and *A. cuneata* about 150 transverse folds. These may be compared with 1-3 folds in *Glycymeris glycymeris*, about 12 folds in *Arca tetragona*, and about 36 folds in *Anadara trapezia* (Atkins, 1936; Sullivan, 1961). The transverse folds are slender and long in *A. cuneata* (Fig. 5C) but thicker and broader in the other two species. The folds of *A. antiquata* (Fig. 3A) are relatively simple and straight, while those of *A. anomala* are wavy (Fig. 4C). (I have observed a similar type of wavy palps in *A. inaequivalvis* (unpublished).) Furthermore, the individual folds also show specific differences. For instance, while the folds remain simple in *A. antiquata*, a ridge occurs at the region of the transverse groove in *A. anomala* and *A. cuneata* (Figs. 3D, 4D and 5D). Moreover, the transverse-fold surface is doubly-grooved in *A. cuneata*. The labial palps of *A. granosa* (Purchon, 1956; and my own observations) reach a stage of complexity intermediate between *A. anomala* and *A. cuneata*.

#### B. Histology

The inner epithelia of all the three species are ciliated, columnar, and variable in height. The epithelia of the outer surface are all cuboidal and are only finely ciliated in *A. cuneata* (Figs. 3B, 4B and 5B). No such inner surface ciliation was observed in *A. trapezia* (Sullivan, 1961). Mucous glands are present in the epithelia of the labial palps of all the species examined. They are unicellular and multicellular. The unicellular mucous glands are of two types, MG1 and MG2. The cytoplasm of MG1 contains few small, indistinct, vacuoles. The cytoplasm of MG2 is very distinctly vacuolated. The multicellular mucous glands or MG3 have vacuolated foamy cytoplasm. The MG1 and MG2 cells are observed in both *A. antiquata* and *A. anomala* (Figs. 3B and 4B) and MG1, MG2 and MG3 cells in *A. cuneata* (Fig. 5B). The MG1, MG2 and MG3 cells are similar in structure to the PA, PB and PC cells of *A. trapezia* as described by Sullivan (1961). In *A. trapezia*, the PC (= MG3) cells occur in the smooth proximal portion of the inner surface, while in *A. cuneata* the MG3 cells occur throughout the outer surface of the labial palp (Fig. 5B).



*The sorting mechanisms*

The sorting mechanisms on the inner surface of the labial palps are similar to those observed by Atkins (1936) for *Arca* and *Glycymeris*, by Sullivan (1961) for *Anadara trapezia*, and Purchon (1956) for *A. granosa*. They all receive particles of food, etc. from the ctenidia and further sortings are conducted on the inner surfaces of the palps (Figs. 3C, 4C and 5C) prior to any entry (of the particles) into the mouth. The main currents (very large arrows in Figs. 3D, 4D and 5D) carrying particles from the ctenidia pass down the upper surface of the palps and leave at the point "X" in Figures 3C, 4C and 5C. As the main currents proceed along, subsidiary ciliary currents of the transverse fold surfaces (large and small arrows on transverse folds in Figs. 3D, 4D and 5D) sort out the rejected particles, passing them on to the current on the outer-edge of the palp. The accepted particles are conveyed to the transverse groove. The outer-edge current collects the rejected particles from all the transverse folds and ferries them to "X." The transverse groove currents (strong arrows in transverse grooves in Figs. 3D, 4D and 5D) join the lateral oral groove current into which they pass the accepted particles. The non-folded surfaces of the proximal portions of the palps have small, rather diffuse, ciliary currents, as shown in Figures 3C, 4C and 5C, where particles are mainly for rejection and are directed towards the position of "X." As in *A. granosa* (Purchon, 1956) there is a strong ciliary current carrying particles collected from the outer surface of the labial palps onto the inner surface at the distal portion in *A. cuneata* (point "Y" in Fig. 5C). This is absent in *A. antiquata* and *A. anomala*, and was not observed by Atkins (1936) and Sullivan (1961) for the species they studied.

*Ciliary currents on the foot and visceral mass*

After removal of the ctenidium and labial palp on one side, the ciliary tracts on the visceral mass and foot were observed. There are dissimilarities among all the three species investigated. The arrangement in *A. antiquata* appears to be somewhat similar to that seen in *Arca tetragona* (Atkins, 1936), where there are discernible dorso-anterior and ventro-posterior tracts. These roughly coincide in position with the two major ctenidial tracts (Fig. 3F). The situation is somewhat modified in *A. anomala*. In this species are a dorsally-directed current, roughly along the position of the mid-portion of the gill lamellae, and a ventro-posterior current (Fig. 4F). A distinct dorso-anterior current is absent in *A. cuneata* (Fig. 5F). The posteriorly directed rejection tract leaves the foot and visceral mass in roughly the same position in all the three species as in *Arca* (Atkins, 1936).

*Ciliary currents on the mantle lobe*

Ciliary currents on the mantle were observed after careful removal of the ctenidia, labial palps, foot and visceral mass.

Basically, the ciliary tracts on the mantle lobe in all the three species examined are similar (Figs. 3G, 4G and 5G). There are present distinct dorso-anterior and ventro-posterior currents not unlike those of *Arca* (Atkins, 1936) and *Anadara trapezia* (Sullivan, 1961). These two currents roughly correspond with the ones

of the ctenidium in position. In *A. cuneata* the ventro-posterior tract is reinforced by a third distinct tract—the mid-posterior. This current gathers the dorso-anterior current ventrally and enters into the ventro-posterior current more posteriorly. In *A. granosa*, although there is no dorso-anterior current on the mantle, a diffuse dorso-posterior flow and a ventro-posterior current occur (Purchon, 1956; my own observations).

The position of rejection from the mantle lobe and subsequent expulsion from the mantle cavity to the exterior lies posteriorly (see Figs. 3G, 4G and 5G) in all the species studied. This more or less coincides with the region of exit of the exhalant current. In *Arca* the point of expulsion happens to be in the region of the posterior inhalant current where particles are consolidated (Atkins, 1936) before ejection through the inhalant opening by “clapping” of the shell valves.

### DISCUSSION

The investigations in the field and the laboratory on the ciliary feeding mechanisms indicate very strongly that the species *Anadara antiquata*, *A. anomala* and *A. cuneata* are well suited to their respective habitats—rocky, sandy, and muddy. The inhalant and exhalant currents leaving and entering the animals show signs of adaptation to the habitats. The rocky-shore form (*A. antiquata*) is the least specialized of the three. Its form, presence of a byssus throughout life, and its three distinct inhalant and exhalant currents (one anterior and two posterior) closely resemble those of *Arca* (Atkins, 1936), which is a more primitive genus than *Anadara*. Yonge (1962) has hypothesized that byssal attachment is primarily a characteristic adaptation of metamorphosing spat, and its retention in some adult bivalves is neotenic.

The sandy-shore form (*A. anomala*) and muddy estuarine form (*A. cuneata*) are more or less specialized, from the evidence of their ciliary feeding mechanisms and associated structures. The “mud” form burrows completely and successfully retains a rather diffuse anterior inhalant current of water which brings in finely stirred-up organic particles in the mud that probably serve as the major food source instead of the plankton. The “sand” form buries itself almost completely, but not quite. A little of the posterior portion of the bivalve is left exposed. This is a plankton feeder and an anterior inhalant stream is impractical and hence absent. Yonge (1955) asserted that (p. 207) “in the Lamellibranchia the inhalant aperture is primitively anterior” when he described the total absence of an anterior inhalant current in *A. senilis*. In this respect, the species *A. anomala* is more “advanced” than *A. cuneata* since the latter still maintains traces of anterior inhalant currents.

Although the species *A. cuneata* is more “primitive” than *A. anomala*, on the basis of position of the inhalant apertures, the former shows more elaborate structures associated with feeding. The ctenidia are comparatively larger in surface area. In *A. cuneata* the labial palps have more than four times the number of transverse folds, and the individual folds are more elaborately grooved and more abundant in variety and quantity of mucous glands than in *A. anomala*. Cilia are present on the outer surface of the labial palps in *A. cuneata* but absent in *A. anomala*. The fine frontal cilia are more numerous in each gill filament in the former species than the latter. Finally, the ciliary currents on the mantle lobe

of *A. cuneata* are more elaborate and there is present a mid-posterior current which is absent in *A. anomala*. All these elaborations of the feeding apparatus in the "mud" species are presumably necessary for the survival in its particular habitat. To cope with an environment of much silt and suspended particles in the surrounding water *A. cuneata* requires a bigger sorting area on the gills, labial palps, more mucous secretion and ciliation of exposed parts. Moreover, in *A. granosa* (Purchon, 1956; my own observations) and in *A. cuneata*, there are additional strong ciliary currents ("Y" in Fig. 5C) on the labial palps.

An interesting feature of ciliary currents on the gills of all members of the Arcacea studied is the presence without exception of a posteriorly directed rejection current on the ventral margin of the gills (Atkins, 1936, on *Arca tetragona* and *Glycymeris glycymeris*; Yonge, 1955, on *Anadara senilis*; Sullivan, 1961, on *A. trapezia*; and my observations on *A. antiquata*, *A. anomala*, and *A. cuneata*). My re-examination of *A. granosa* indicates the presence of this feature, contrary to the negative findings of Purchon (1956). Presumably this is a universal character of the family Arcidae, and possibly of the superfamily Arcacea. Except for the Anomiacea (Atkins, 1936; Yeo, personal communication) the presence of the ventro-posterior rejection current has not been found elsewhere in the Bivalvia. The separation of the Subclass Protobranchia (Order Nuculacea) from the Subclass Lamellibranchia (including Arcacea and many other more typical lamellibranchiate bivalves) is firmly based on paleontological and functional grounds (see Cox, 1959; Yonge, 1959). However, the taxodont dentition of the arcids probably has phylogenetic significance *within* the Subclass Lamellibranchia. On the other hand, the similarities of rejection currents in the anomiids and the arcids are probably totally independent in evolution, and of functional, rather than *phyletic*, significance.

#### SUMMARY

1. The ciliary feeding mechanisms of a rocky- (*A. antiquata*), sandy- (*A. anomala*), and muddy- (*A. cuneata*) habitat species of *Anadara* are observed.
2. Adaptive differences are found for the three species in their inhalant/exhalant apertures, structures and ciliary surfaces associated with feeding.
3. Some primitive and specialized features of the three species in relation to their feeding mechanisms are discussed.
4. Observations of the ciliary feeding currents were also made on *Anadara granosa*.
5. The ciliary tract on the ventral margin of the ctenidium is directed posteriorly in *A. granosa*, contrary to previous observation.

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